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A New North American Species of *Pogonomyrmex* (Hymenoptera: Formicidae) from the Mohave Desert of Eastern California and Western Nevada

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Abstract.—***Pogonomyrmex mohavensis* Johnson sp. nov.** is described from the Mohave Desert of eastern California and western Nevada, USA. A mitochondrial phylogeny affirmed taxonomic validity of *P. mohavensis,* and inferred that it is most closely related to *Pogonomyrmex snellingi.* Field observations and a distribution map for *P. mohavensis* are also provided, along with an updated key to *Pogonomyrmex californicus* group species that occur in central and western North America. *Pogonomyrmex mohavensis* can be separated from other *P. californicus* group species based on a unique combination of characters that include: (1) six mandibular teeth (very rarely with a small seventh denticle), and (2) in side view, the cephalic rugae extend more or less directly to the vertex and do not converge posterior to the eyes or form circumocular whorls. All other *P. californicus* group species have 7–8 mandibular teeth (six in *Pogonomyrmex anzensis*) and the cephalic rugae almost always converge posterior to the eyes or form circumocular whorls.

Key words.—*Pogonomyrmex,* new species, Mohave Desert, *P. californicus* species group, mitochondrial phylogeny

The seed-harvester ant genus *Pogonomyrmex* Mayr, 1868 is an exclusively New World group that consists of approximately 64 described species (Bolton et al. 2006; Lattke 2006) that occur throughout much of North and South America. In the American West, Mexico, and southern South America, these are ecologically dominant ants, especially in arid habitats. The modern study of the genus began with Cole's (1968) stellar revision of North American species. This monograph stabilized the taxonomy of this group and set the stage for studies of ecology, biogeography, territoriality, mating behavior, communication, caste determination, and foraging behavior that have greatly facilitated our understanding of ant biology (Anderson et al. 2006; Gadau et al. 2003; Hölldobler 1976a, 1976b; Johnson 2000, 2001; Taber 1998). Since the publication of Cole's study, several additional new species have been described from North America and perhaps several more remain to be discovered, especially in Mexico (e.g., Vásquez-Bolaños and MacKay 2004). This paper describes a new species of *Pogonomyrmex* from the Mohave Desert of eastern California and western Nevada, USA.

MATERIALS AND METHODS

Measurements and Indices

Morphological characters were photographed using a Spot Insight QE camera attached to a Leica MZ 125 microscope. Images were then projected onto a video monitor, and characters were measured using ImageJ (available at http://rsb.info.nih.gov/nih-image/). Measurements were calibrated using photographs of an ocular micrometer scaled in 0.01 mm increments. The following standard measurements are used:

HL	**Head Length**: length of the head capsule excluding mandibles, in full-face view, from the midpoint of the anterior cly-

	peal margin to the midpoint of the occipital margin.
HW	**Head Width**: maximum width of the head immediately behind the eyes, measured in full-face view.
CI	**Cephalic Index**: (HW/HL) × 100.
MOD	**Maximum Ocular Diameter**: maximum diameter of the eye measured with the head in full lateral aspect.
OI	**Ocular Index**: (MOD/HW) × 100.
OMD	**Oculo-Mandibular Distance**: minimum distance from the anterior eye margin to the nearest point of the malar area (base of mandible).
SL	**Scape Length**: maximum straight line length of the antennal scape from apex to base.
SI	**Scape Index**: (SL/HW) × 100.
PNW	**Pronotal Width**: maximum width of the pronotum, as seen from above, measured at a right angle to the longitudinal axis of the mesosoma.
HFL	**Hind Femur Length**: measured along the dorsal margin from the articulation with the trochanter to most distal tip of the femur.
HFI	**Hind Femur Index**: (HFL/HW) × 100.
ML	**Mesosoma Length**: diagonal length of the alitrunk in profile from the point at which the pronotum meets the cervical shield to the posterior base of the metapleural lobe.
PW	**Petiole Width**: maximum width of petiole, as seen from above, at a right angle to the longitudinal axis of the mesosoma.
PPW	**Postpetiole Width**: maximum width of postpetiole, as seen from above, at a right angle to the longitudinal axis of the mesosoma.

Abbreviations of Depositories

CASC	California Academy of Sciences, San Francisco, California, USA
CIDA	Orma J. Smith Museum of Natural History, The College of Idaho, Caldwell, Idaho, USA
LACM	Los Angeles County Museum of Natural History, Los Angeles, California, USA
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
RAJC	Robert A. Johnson collection, Tempe, Arizona, USA
UCDC	Bohart Museum of Entomology, University of California, Davis, California, USA
USNM	National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
WPMC	William P. MacKay collection, El Paso, Texas, USA

Molecular Analyses and Phylogenetic Inferences

We constructed a phylogeny using a 653 base-pair sequence of the cytochrome oxidase I mitochondrial gene to affirm taxonomic status of *P. mohavensis* and to infer its relationship with other species in the *P. californicus* group. The phylogeny included multiple samples from sympatric colonies of *P. mohavensis* and *P. californicus*, with the latter species being the only other *P. californicus* group species that occurred at or near the type locality; samples of the four other species in the *P. californicus* group were also included (Table 1). We also included samples of *P. anzensis*, whose placement is unclear because it has been suggested to belong to the *P. occidentalis* group (Cole 1968) and the *P. californicus* group (Parker and Rissing 2002; Taber 1990).

Individuals were removed from the ethanol, then crushed in 100 µl 5% Chelex (in TE pH 8.0) and 1 µl proteinase K (5 mg/mL) was added. Samples were then

Table 1. Locale data (state: county, locale) for specimens in the genus *Pogonomyrmex* that were used to construct the mitochondrial phylogeny (see Figure 3). All locales are in the United States, except as noted.

Taxon and locality	Latitude	Longitude	Elevation (m)	Collector and accession number
P. anzensis Cole				
CA: San Diego: Anza Borrego State Park, Split Mountain	33° 01′N	116° 07′N	260	SP Cover #4807
CA: San Diego: Borrego Mountains	33° 10′N	116° 10′N	240	SP Cover #4821
P. californicus (Buckley)				
CA: Inyo, Alabama Hills at 7.5 km W Lone Pine	36° 36′N	118° 09′N	1540	RA Johnson #4127, 4128, 4132, 4133, 4134
CA: Inyo, Alabama Hills, 7.8 km S Jct Horseshoe Meadows & Whitney Portal Rds	36° 31′N	118° 06′N	1625	RA Johnson #4137, 4138
NV: Clark, 5.0 km E Jean	35° 46′N	115° 16′N	840	RA Johnson #4224
P. comanche Wheeler				
TX: Tarrant, Ft Worth Wildlife Refuge	32° 51′N	97° 28′N	180	AB Mayo #3985
P. magnacanthus Cole				
AZ: La Paz, 15.5 km E Tacna, Mohawk Dunes	32° 42′N	113° 47′N	140	RA Johnson #2235
CA: Riverside: Palm Desert, Bob Hope & Gerald Ford Dr	33° 47′N	116° 24′N	75	RA Johnson #1005
CA: San Diego: Anza Borrego, 8.0 km S Split Mtn	32° 59′N	116° 09′N	260	GC Snelling #98-052
P. maricopa Wheeler				
AZ: Pima, San Xavier Mission	32° 06′N	111° 00′W	770	CP Strehl #26
P. mohavensis Johnson				
CA: Inyo, Alabama Hills at 7.5 km W Lone Pine	36° 36′N	118° 09′N	1540	RA Johnson #4129, 4130
CA: Inyo, Alabama Hills, 1.3 km S Jct Horseshoe Meadows & Whitney Portal Rds	36° 35′N	118° 07′N	1450	RA Johnson #4135, 4136, 4145, 4146
NV: Nye, Highway 374 at Rhyolite	36° 53′N	116° 49′N	1090	RA Johnson #4218
P. snellingi Taber				
Mexico: Baja California, 9.6 km N Guerrero Negro	28° 04′N	114° 01′W	5	RA Johnson #2663
Mexico: Baja California Sur, Vizcaino Desert	27° 47′N	113° 34′W	65	RA Johnson #3032

incubated at 57° C for 1 hour and subsequently heated to 95° C for 5 min, then centrifuged at 14,000 rpm for 10 min. The supernatant containing isolated DNA was then stored.

We amplified partial mitochondrial cytochrome oxidase I sequences using the LCO/HCO primers in a 25 µl reaction volume containing 0.01 units of Taq polymerase, 5 µl of 5× Go Taq Buffer, 1 µl $MgCl_2$ (50 mM), 1 µl dNTPs (10 mM), and 13.9 µl of H_2O. The locus was amplified using the following PCR program: an initial 4 min at 95° C, 38 cycles of 95° C for 30 sec, 45° C for 45 sec, and 68° C for 1.5 min, and finally 68° C for 4 min. PCR samples were purified using exonuclease I and shrimp acid phosphatase (ExoSAP-IT, USB Corporation, Cleveland, Ohio, USA) for digestion of single-stranded DNA (primers) and dNTPs. Samples were sent to the School of Life Sciences core DNA laboratory at Arizona State University and sequenced using an Applied Biosystems 3730 capillary sequencer.

Sequences were aligned using the auto-alignment function in the program Sequencher version 4.6 (Gene Codes Corporation, Ann Arbor, MI). Phylogenetic trees were constructed with both neighbor-joining and maximum parsimony methods using the program Molecular Evolutionary Genetics Analysis (MEGA) Software Version 4.0 (Tamura et al. 2007). Both analyses were in complete agreement for all nodes and so the neighbor-joining tree was used in order to display branch lengths. Bootstrap values were calculated using 1000 pseudoreplicates and ten random taxon additions per replicate, then mapped onto the neighbor joining tree.

RESULTS

Pogonomyrmex mohavensis Johnson, n sp.
(Figs 1A–E)

Worker description.—Head subquadrate (CI = 97.0–104.5), broadest just posterior to eye; posterior margin flat in full-face view. Longitudinal cephalic rugae prominent, in full-face view median rugae diverging only slightly towards the posterior corners of the head. In side view, rugae posterior to eyes not converging or forming circumocular whorls, but rather extending to vertex. Vertex rugose, with rugae often becoming weak or absent on posterior corners. Cephalic interrugal spaces slightly punctate, moderately to strongly shining. Anterior margin of clypeus flat to slightly concave. Mandible with six teeth, a seventh occasionally present as a denticle or very small tooth between the basal and subbasal teeth (76% had six teeth on both mandibles, 17% had an additional denticle on one mandible, 7% had an additional denticle on both mandibles, *n* = 98). Mandibular dorsum coarsely striated. MOD ranging from 0.21–0.24× HL. Eyes in profile situated slightly posterior to middle of head, OMD = 1.2–1.6 MOD. Antennal scapes relatively long (SI = 72–82), reaching to or surpassing vertex by less than the length of the basal funicular segment. Basal flange of scape flattened and very well-developed, at least partially translucent near margin. Psammophore well developed.

Mesosomal profile flattened to slightly convex. All mesosomal surfaces with prominent parallel/subparallel rugae. Dorsum of promesonotum with transverse rugae that curve obliquely to posterior on the pronotal sides, or rugae traverse obliquely from anterior to posterior. Mesopleura with transverse rugae angling posteriodorsally. Propodeum lacking spines or teeth, in side view evenly convex; rugae on propodeal dorsum transverse, posterior face of propodeum smooth and shining. Propodeal spiracles narrowly ovate. Interrugal spaces on mesosoma smooth and shining to slightly punctate and moderately shining. Legs moderately to strongly shining.

Petiolar peduncle long, ventral surface usually smooth, lacking tooth or lobe, occasionally with small angular process. In side view, petiolar node broadly but asymmetrically rounded with anterior surface notably shorter than posterior surface. Apex of node rounded, sometimes weakly angulate. In dorsal view, petiolar node longer than broad, widest anteriorly. Sides and dorsum of petiolar node moderately punctate, subshining, sculpture on dorsal surface variable: either lacking rugae, or with few transverse rugae, or up to several longitudinal rugae. Dorsum of postpetiole convex in profile; in dorsal view, widest at or near posterior margin and tapering to anterior margin, maximal width about equal to length, moderately punctate, subshining. Gaster smooth and shining.

Erect whitish pilosity moderately abundant on head, variable in length, longest hairs not exceeding MOD. Moderately abundant suberect to semidecumbent pilosity on scape, abundant semidecumbent hairs on funicular segments. Legs with moderately abundant suberect white setae. Mesosoma, petiole, and postpetiole with moderately dense erect to flexuous white setae, often similar in length, longest reaching to or slightly exceeding MOD; gastric tergites with more abundant, slightly shorter pilosity. Entire body concolorous ferruginous orange, or with gaster sometimes slightly lighter or darker than rest of body, but never black.

Worker measurements.—Holotype (paratypes, *n* = 12, notation: minimum-maximum). All measurements are in millime-

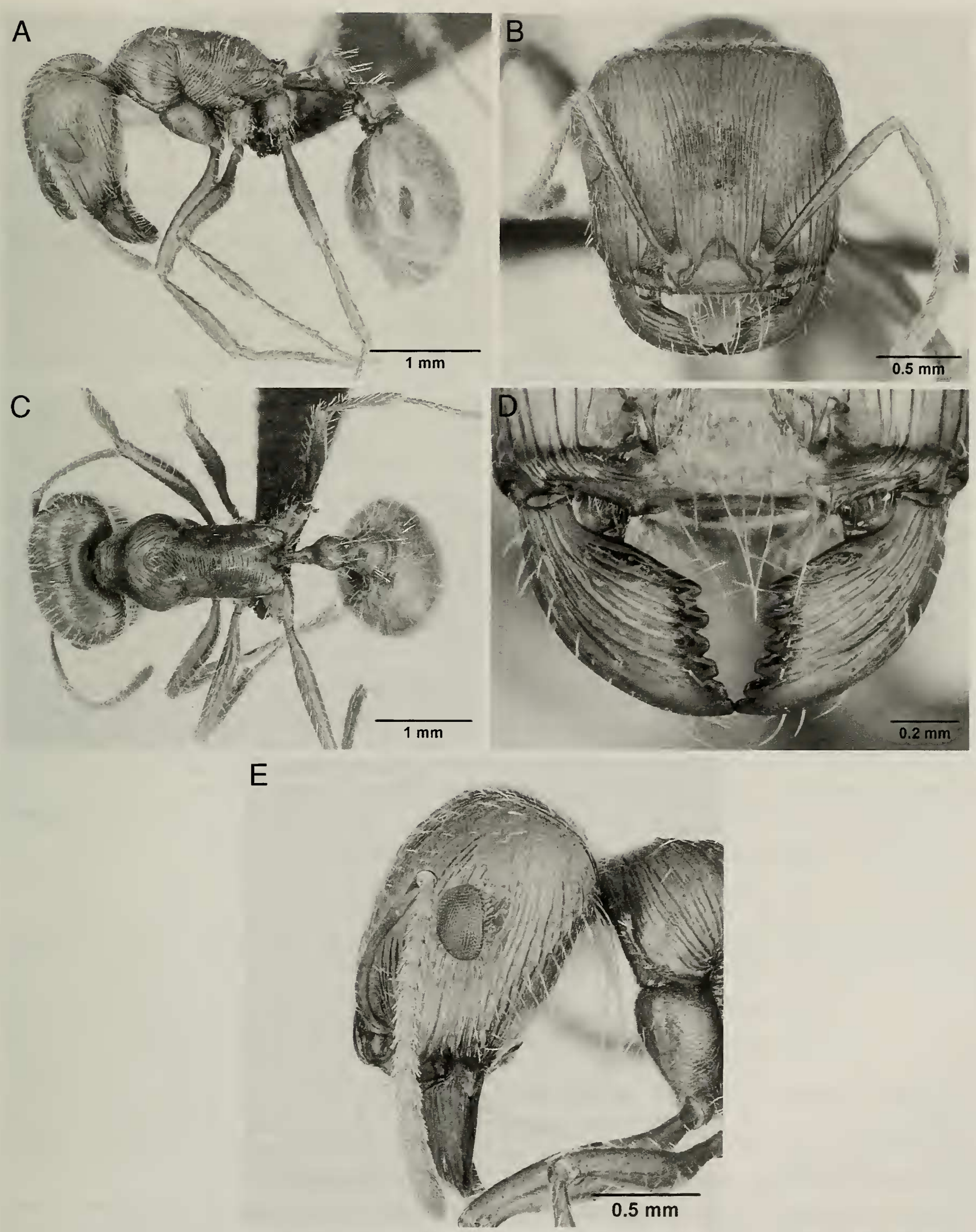

Fig. 1. *Pogonomyrmex mohavensis* Johnson – PARATYPE WORKER. **(A)** lateral view of worker body, **(B)** frontal view of worker head, **(C)** dorsal view of worker body, **(D)** frontal view of worker mandible with six teeth, plus a small denticle between the left basal and subbasal teeth, and **(E)** cephalic rugae extending to vertex, not forming circumocular whorls posterior to eyes.

ters. HL 1.56 (1.35–1.63); HW 1.61 (1.31–1.67); MOD 0.37 (0.30–0.37); OMD 0.46 (0.36–0.50); SL 1.14 (0.94–1.21); PNW 0.98 (0.85–1.04); HFL 1.65 (1.21–1.71); ML 1.90 (1.60–1.99); PW 0.40 (0.31–0.41); PPW 0.52 (0.45–0.56). Indices: SI 70.81 (70.06–81.75); CI 103.21 (97.04–104.55); OI 22.98 (20.95–24.82); HFI 102.48 (92.37–110.53).

Queen.—Unknown.

Male.—Unknown.

Diagnosis.—*P. mohavensis* is likely to be confused only with *P. californicus* but may be distinguished by the following characters: (1) *P. mohavensis* is slightly smaller (HW = 1.31–1.67) than sympatric *P. californicus* (HW = 1.22–1.78), (2) *P. mohavensis* has six mandibular teeth (a seventh sometimes occurs as a denticle between the basal and subbasal teeth), and (3) in side view, the cephalic rugae extend more or less directly to the vertex and do not converge posterior to the eyes or form circumocular whorls. In *P. californicus*, the mandible has seven more or less normally sized teeth and the cephalic rugae converge posterior to the eye, sometimes forming circumocular whorls. In addition, in some populations of *P. californicus* (including the population at the type locality of *P. mohavensis*) the gaster is dark brown to black. In *P. mohavensis*, the gaster is concolorous with the head and mesosoma, or sometimes a bit darker, but never dark brown to black.

In some specimens of both *P. californicus* and *P. mohavensis*, the cephalic rugae become weak or may even more or less disappear directly posterior to the eye, making evaluation of this sculptural character difficult, especially if magnification is low or the lighting is not good. In these cases, it appears that the number of mandibular teeth can secure separation. Even in examples of *P. mohavensis* with seven mandibular teeth, the extra tooth is much smaller than the flanking basal and subbasal teeth. This seventh tooth is fully developed in *P. californicus* and is subequal in size with the flanking teeth. Also note that substantial mandibular wear is common in older *Pogonomyrmex* workers, such that it is strongly recommended that at least several workers from each colony series be examined when attempting identification.

Type material.—Holotype (worker) plus 123 paratypes. **USA:** ***California***: *Inyo Co.*: Alabama Hills, 1.3 km S Junction Horseshoe Meadows & Whitney Portal Roads, 1450 m (36° 34.8′N 118° 7.1′W), 24 May 2008, leg. R.A. Johnson #4136. Nests were in mixed Mohavean Desert woody scrub habitat; dominant plant species included *Acamptopappus sphaerocephalus, Atriplex polycarpa, Atriplex canescens, Hymenoclea salsola, Grayia spinosa, Krascheninnikovia lanata, Eriogonoum fasciculatum, Coleogyne ramosissima, Ephedra* sp., *Gutierrezia* sp., *Lycium* sp., and *Cuscuta* sp. The holotype is deposited in the MCZ. Paratypes (*n* = 123 workers) all from the same locality and date as the holotype and leg. R.A. Johnson #4136 are distributed as follows: 3w CIDA, 9w CASC, 9w LACM, 15w MCZ, 9w UCDC, 12w USNM, 6w WPMC, 15w RAJC. Additional paratype series (RAJC) include RAJ #4135 (12w), #4145 (15w), and #4146 (24w); all series have additional workers in ethanol.

Additional material.—**USA:** ***California***: *Inyo Co.*: Alabama Hills at 7.5 km W Lone Pine, 1540 m, 23 May 2008 (36° 35.6′N 118° 8.5′W) (R.A. Johnson RAJ #4129, 15w; #4130, 6w; RAJC), Alabama Hills at 6.4 km W Lone Pine, 4950′, 14 May 2006 (R.R. Snelling #06-007, 1w; RAJC), Artists Drive, Death Valley National Monument, 800 feet, 29 Apr. 1952 (CR-537, 9w; LACM). *Kern Co.*: 20 mi N Bakersfield, 5 Aug. 1959 (A.C. Cole CAL-345, 16w; LACM). ***Nevada***: *Nye Co.*: Hwy 374 at Rhyolite, 1090 m, 18 Apr. 2009 (R.A. Johnson, RAJ #4218, 3w; RAJC), Rock Valley at 9 mi ENE Lathrop Wells, 14 Apr. 1970 (G. & J. Wheeler NEV-777, 3w; LACM). Figure 2 shows the known geographic distribution of *P. mohavensis*.

Etymology.—The specific epithet, *mohavensis*, is derived from this species occurring in the Mohave Desert.

Phylogenetic data

The mitochondrial phylogeny affirmed the taxonomic status of *P. mohavensis*, especially given that it is distantly related to sympatric colonies of *P. californicus*

Fig. 2. Geographic distribution of *Pogonomyrmex mohavensis* Johnson; the type locality is denoted by the larger filled black circle.

(Figure 3). The phylogeny also inferred that *P. mohavensis* is most closely related to *P. snellingi,* which is endemic to the peninsula of Baja California, Mexico, and that *P. mohavensis, P. snellingi,* and *P. magnacanthus* comprise a clade of species that are restricted to hot desert habitats of North America. *Pogonomyrmex anzensis* was distantly related to other species in the *P. californicus* group, but we did not include any outgroup species, and thus could not determine if *P. anzensis* belongs in this species group (see also Parker and Rissing 2002). Overall, note that the phylogenetic relationships provided herein, as well as those in Parker and Rissing (2002) and Taber (1990, 1998), should be considered tentative. Better resolution of these species relationships requires a multiple gene phylogeny, which we are in the process of completing.

BIOLOGY AND DISCUSSION

The large series of workers collected during this study, combined with collections of sympatric *P. californicus* and a mitochondrial phylogeny of *P. mohavensis* and congeners in the *P. californicus* species group, make a formal description possible and confirm that *P. mohavensis* is a valid species. Based on dentition, *P. mohavensis* is not the undescribed species that has been known to exist for about twenty years and has been referred to by some authors as *Pogonomyrnmex* sp. B (Johnson 2000; Taber 1990, 1998); *P. mohavensis* has six teeth (this

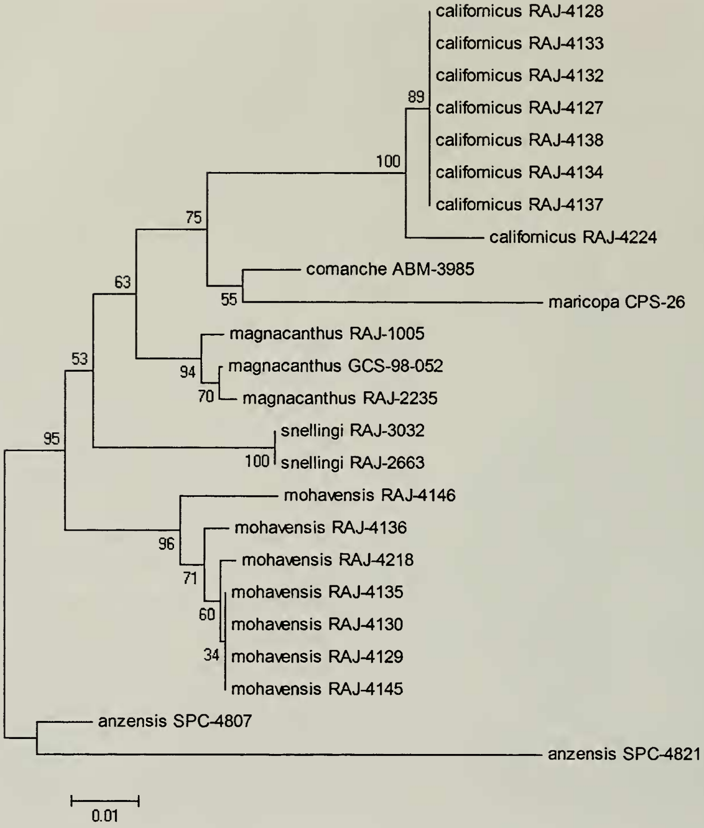

Fig. 3. Neighbor-joining tree for species in the *Pogonomyrmex californicus* group based on a 653 base-pair sequence of the cytochrome oxidase I gene. Numbers on branches represent bootstrap values based on 1000 pseudoreplications. The scale bar depicts expected rate of substitutions per site. Numbers following each species name refer to the accession number of the series from which the individual was taken; locale data for each series are given in Table 1.

study), whereas *P.* sp. B has seven teeth (Taber 1990, 1998).

Nests of *P. mohavensis* consist of a small circular tumulus that ranges from 7.5–13 cm in diameter; the shape is evenly symmetrical and lacks the crescentic shape typical of *P. californicus*. Nests were difficult to locate because of their low density and the small size of their tumulus; nests were most easily located by baiting foragers, then following them back to the nest. Nests were placed in various situations that included open exposed sites, under the edge of small bushes, and under dried cow dung. *Pogonomyrmex mohavensis* was sympatric with *P. californicus* at one site, and with *P. rugosus* at the other. Workers of *P. mohavensis* foraged solitarily during the day, harvesting seeds and related items. Partial excavation of nests indicated that colonies reach a maximum size of about 600–700 workers.

Males and females are unknown, but sexual larvae and pupae were excavated from multiple nests on 24 May, 2008, indicating that reproductive sexuals begin maturing by mid-June. Mating flights are predicted to be similar to those of *P. californicus*, in which flights are triggered by photoperiod (not rain-triggered as in most other species of *Pogonomyrmex*) (Johnson 2000) and likely take place over a 2–3 week period during early summer.

Current records suggest that *P. mohavensis* is restricted to areas in and near the Mohave Desert at elevations from 245–1540 meters (Figure 3). Three series of specimens found during this study were obtained by examining series of *P. californicus* (CASC, LACM, UCDC) because Roy Snelling had suggested that material of the new species had likely been misidentified as *P. californicus*. I also found one series of *P. mohavensis* that had been misidentified as *P. magnacanthus* (LACM). Moreover, *P. mohavensis* appears to be relatively uncommon compared to *P. californicus*.

KEY TO THE WORKERS IN THE *POGONOMYRMEX CALIFORNICUS* SPECIES GROUP FROM CENTRAL AND WESTERN NORTH AMERICA

(*P. anzensis* is included, though it may not belong in this species group).

1	Basal tooth strongly offset from basal margin; diastema present between basal and subbasal teeth, mandible sometimes with eight teeth when very small tooth occurs in diastema	*snellingi*
–	Basal tooth not strongly offset, lacking diastema between basal and subbasal teeth	2
2(1)	Dorsum of petiolar node, viewed from side, distinctly flattened, and viewed from above, with strong widely spaced wavy, subparallel, transverse rugae and usually distinct, broad, shallow, longitudinal depression; propodeum armed with short to long spines; cephalic interrugal punctures prominent	*comanche*
–	Dorsum of petiolar node, viewed from side, not flattened, and viewed from above, lacking strong, widely spaced, wavy, subparallel, transverse rugae and broad, shallow longitudinal depression; propodeal armature present or absent; cephalic interrugal punctures absent to prominent	3
3(2)	Eye unusually large (OI = 29–33), eye length slightly less than to notably more than oculo-mandibular distance (distance between lower margin of compound eye and nearest point of base of mandible); relatively small ant (4.7–5.2 mm)	*magnacanthus*
–	Eye small (OI = 18–24), eye length notably less than oculo-mandibular distance; usually larger ant (5.5–8.7 mm)	4
4(3)	Propodeal spines absent or with a pair of angles, denticles, or short to long spines; cephalic interrugal punctulation rather strong; interrugal punctulation of epipleura moderate to strong; interrugal spaces subopaque	*maricopa*
–	Propodeal spines absent; cephalic interrugal punctulation absent to moderate; interrugal punctulation of epipleura very weak or absent; interrugal spaces moderately to strongly shining	5
5(4)	Mandible with six teeth; posterior corners of head bearing a prominent longitudinal, strongly carinate ruga which is well set off from the outer portion of the occipital corner; in lateral view, ventral lobe of postpetiole with a strong triangular, ventral tooth	*anzensis*
–	Mandible with six or seven teeth; posterior corners of head lacking a prominent longitudinal ruga; in lateral view, ventral lobe of postpetiole lacking a ventral tooth	6
6(5)	Mandible always with seven teeth and cephalic rugae converging posterior to eyes in side view, often forming circumocular whorls	*californicus*
–	Mandible with six teeth, a seventh *small* tooth sometimes present between basal and subbasal teeth and the cephalic rugae extending to vertex in side view, not converging posterior to eyes or forming circumocular whorls	*mohavensis*

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LITERATURE CITED

Anderson, K. E., J. Gadau, B. M. Mott, R. A. Johnson, A. Altamirano, C. Strehl, and J. H. Fewell. 2006. Distribution and evolution of genetic caste determination in *Pogonomyrmex* seed-harvester ants. *Ecology* 87: 2171–2184.

Bolton, B., G. A. Alpert, P. S. Ward, and P. Naskrecki. 2006. *Bolton's Catalogue of Ants of the World: 1758–2005*. Harvard University Press, Cambridge, Massachusetts.

Cole, A. C. 1968. *Pogonomyrmex Harvester Ants: A Study of the Genus in North America*. University of Tennessee Press, Knoxville.

Gadau, J., C. P. Strehl, J. Oettler, and B. Hölldobler. 2003. Determinants of intracolonial relatedness in *Pogonomyrmex rugosus* (Hymenoptera: Formicidae): mating frequency and brood raids. *Molecular Ecology* 12: 1931–1938.

Hölldobler, B. 1976a. The behavioral ecology of mating in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behavioral Ecology and Sociobiology* 1: 405–423.

———. 1976b. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behavioral Ecology and Sociobiology* 1: 3–44.

Johnson, R. A. 2000. Seed-harvester ants (Hymenoptera: Formicidae) of North America: an overview of ecology and biogeography. *Sociobiology* 36: 89–122 + 83–88.

———. 2001. Biogeography and community structure of North American seed-harvester ants. *Annual Review of Entomology* 46: 1–29.

Lattke, J. E. 2006. A new species of *Pogonomyrmex* (Hymenoptera: Formicidae) from gallery forests of the Orinoco watershed, Venezuela. *Myrmecologische Nachrichten* 8: 53–57.

Parker, J. D. and S. W. Rissing. 2002. Molecular evidence for the origin of workerless social parasites in the ant genus *Pogonomyrmex*. *Evolution* 56: 2017–2028.

Taber, S. W. 1990. Cladistic phylogeny of the North American species complexes of *Pogonomyrmex* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 83: 307–316.

———. 1998. *The World of the Harvester Ants*. Texas A&M University Press, College Station.

Tamura, K., J. Dudley, M. Nei, and S. Kumar. 2007. MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. *Molecular Biology and Evolution* 24: 1596–1599.

Vásquez-Bolaños, M. and W. P. MacKay. 2004. Una especie nueva de la hormiga cosechadora del género *Pogonomyrmex* (Hymenoptera: Formicidae) de México. *Sociobiology* 44: 283–287.